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Climate change, climatic variation, and extreme
biological responses

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Extreme climatic events could be major drivers of biodiversity change, but it is unclear whether extreme biological changes are (i) individualistic (species- or group-specific), (ii) commonly associated with unusual climatic events and/or (iii) important determinants of long-term population trends. Using population time series for 238 widespread species (207 Lepidoptera and 31 birds) in England since 1968, we found that population ‘crashes’ (outliers in terms of species’ year-to-year population changes) were 46% more frequent than population ‘explosions’. (i) In every year, at least three species experienced extreme changes in population size, but these were expressed in different directions in 41 of the 44 years considered, suggesting individualistic responses to different, short-term events, most likely associated with climatic variability. We found some degree of synchrony (crash or explosion in a given year) within Lepidoptera, but not among bird species, and we found no agreement between the two groups. (ii) Six out of 44 years showed a significant excess of species experiencing crashes (four years for Lepidoptera, one for birds) or explosions (one year for Lepidoptera). These ‘consensus years’ were associated with climatically-extreme years, consistent with a link between extreme population responses and climatic variability, although not all climatically-extreme years generated excess numbers of extreme population responses. (iii) Links between extreme population changes and long-term population trends were absent in Lepidoptera and modest (but significant) in birds. We conclude that extreme biological responses are individually linked to climate, but that long-term trends of widespread species have not, to date, been dominated by these events.

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1. Introduction

Climate is an important determinant of species range, population change, abundance, phenology and biotic interactions (1-4). The precise sequence of climatic events and the time of year when these events occur may affect whether a species' biological response is rapid lifecycle development and increased reproduction leading to population growth, or increased mortality leading potentially to extinction. In the context of this paper, climate change represents a change to the frequency, severity and sequences of different weather events, which may lead to increases in the frequency of some forms of extreme events such as those associated with heat, drought or flooding, but decreases in others, such as those associated with cold (5). It has been suggested that such extreme events may generate substantial population responses and community transitions, and that these rare events could be as important in determining ecological responses to climate change as are long-term changes to the average climatic conditions that a population experiences (6). However, rigorous assessment of the frequencies and impacts of extreme population responses are constrained by the limited availability and spatial/taxonomic coverage of long-term population data (7), and also because a given sequence of climatic events will not necessarily generate a consensus response in organisms (6) due to inter-specific differences in species' ecological traits and sensitivity to climate. Previous studies have highlighted the individualistic nature of species' responses to different aspects of the climate at different times of year (8-11) although, in general, such studies have focussed on describing responses to climatic means, rather than extremes. Here, we assess the extent to which extreme population responses are individualistic, and evaluate whether they are important determinants of long-term population trends.

Extreme climatic events (ECEs), by their very nature, are outside of the norm experienced by organisms and to which species may be (locally) adapted. As such, we hypothesise that extreme events are more likely to drive negative rather than positive population changes. Therefore, we also assess whether extreme species' responses are more frequently negative, and whether these events are commonly associated with unusual climatic conditions. Previous approaches to understanding the importance of ECEs for biological communities have been either to identify such an event (e.g. a drought) and then see if some or many species responded to it or, alternatively, to seek an explanation for one-off extreme population changes that have been observed (12). Such studies have provided strong evidence of population crashes in response to unusual climatic conditions, especially in relation to extreme droughts, winter freezing, unseasonal cold and excessive heat (5, 13-19, cf. coral reef bleaching and anoxia in aquatic systems [20, 21]). However, there is potential that the results could be unrepresentative if the choice of year, climatic event or species under consideration have

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53 been influenced by the events themselves. Hence, the choice of study species may not be appropriate
54 to elucidate the frequencies of rare events or their long-term importance during a period of climatic
55 change. As Bailey & van de Pol (6) and van de Pol et al. (22) discuss, a major drawback of many
56 studies linking ecological and climatic extremes has been a focus on the impacts of single climatic
57 events, over short time periods, leaving questions remaining about the long-term implications of
58 extreme events (but see 23). Here, we remove these potential biases by taking a multi-species
59 approach, analysing data over a relatively long, continuous time period to find out whether extreme
60 population changes tend to take place in years that are also climatically extreme. To do this, we
61 utilise long-running population dynamic data at a national scale for 238 species from two broad
62 taxonomic groups (31 birds and 207 Lepidoptera in England), to identify group- and species-specific
63 differences in population responses to ECEs. We identify years when species show unusually high
64 levels of population growth or decline, and assess whether those years are associated with particular
65 climatic conditions in the same and/or in the previous year(s).

66 Population growth rates of species with similar life histories (e.g. clutch sizes or survival rates) have
67 the potential to be highly synchronised (24, 25), while differences in life history can desynchronise
68 dynamics across species (24, 25). Thus, we contrast the timing of extreme responses of birds and
69 Lepidoptera, with the expectation that we will observe similar temporal responses within, but not
70 between, these two taxonomic groups. We also identify years where an unusually large proportion of
71 species exhibit extreme population changes, and investigate the role of climate in driving these
72 community-wide responses. Although the importance of ECEs to population dynamics is widely
73 discussed in the ecological and climate change literatures (6), the extent to which these events do or
74 do not predict long-term population trends has not been assessed robustly. There is no necessary link
75 between the two, although there is certainly the potential for ECEs to cause long-term population
76 changes (e.g. 26). There may be no link because extreme events, by definition, are rare, and an
77 extreme change in one year may have very little impact on the average rate of population growth or
78 decline over a longer period. Alternatively, it is possible that the cessation of some kinds of ECEs
79 (which previously either constrained populations, or generated periodic increases in reproduction)
80 may be as important to long-term population changes as an increased frequency of previously-rare or
81 wholly novel conditions. The influence of such events may only be seen in population time-series of
82 long duration. Therefore, we consider empirically whether the long-term population trends of species
83 (over four decades) are linked to the extreme population responses that they exhibit over the entire
84 period.

For linguistic simplicity, throughout this article we refer colloquially to population ‘crashes’ (steep year-to-year national population declines – see *Methods*), population ‘explosions’ (rapid increases), ‘bad years’ (years in which crashes take place), ‘good years’ (years in which explosions take place), ‘consensus bad years’ and ‘consensus good years’ (years with a significant excess of population crashes or explosions, respectively). We consider the hypotheses that:

- i. most years are associated with extreme population changes in some species (because biological responses to the environment differ among individual species and between higher taxonomic groups);
- ii. population crashes tend to be more frequent than population explosions during periods of rapid climatic change (as new environments are experienced), and crashes are more extreme than explosions (because the latter are constrained by the intrinsic rate of population growth whereas, in principle, all individuals could die simultaneously);
- iii. consensus years are associated with unusual climatic conditions in the same or previous year; and
- iv. long-term population trends are correlated with extreme population responses.

2. Material and Methods

We define our study area as mainland England, chosen because a large quantity of reliable, long-running annual count data for birds and Lepidoptera (butterflies and macro-moths) are available at this spatial extent. Although Lepidoptera data are also available from the rest of the United Kingdom, we restricted our analyses to match the spatial extent of the bird data, so that the two groups could be directly compared. We conducted our analyses using *R*, version 3.1.0 (27).

(a) Species data

We obtained species data for butterflies, moths and birds from the UK Butterfly Monitoring Scheme (UKBMS; 28), the Rothamsted Insect Survey (RIS; 29), the Common Bird Census (CBC; 30) and the Breeding Bird Survey (BBS; 31). These schemes are national networks of standardised count surveys using either territory mapping (CBC), fixed-location line transects (UKBMS and BBS) or fixed-location light traps (RIS). Butterfly count data (species' abundances for individual sites each year) were collected from 1665 sites spanning the years 1976–2012. Macro-moth count data (species' abundances for individual sites each year) were from 295 sites spanning the years 1968–2012. National population indices of birds spanned the years 1968–2012, combining data from the CBC, which ended in 2000, with data from the BBS which started in 1994 (see 10). There were no bird data for the year 2001 because foot-and-mouth disease severely restricted access in that year.

We included butterfly and moth species for which there were at least five sites with non-zero counts in every year of the time series (37 years for butterflies and 45 for macro-moths), and birds which were sufficiently well monitored by both CBC and BBS surveys. Migrant birds and true-migrant Lepidoptera were excluded, because extreme population changes of such species may not be a result of climate experienced solely in our study area, although the English populations of the most mobile species will still experience some exchanges with regions outside the study region. Thus, we included 178 macro-moth species, 29 butterfly species and 31 bird species in our analyses (listed in Supplementary Table 1). Butterflies and moths were analysed together as they belong to one taxonomic order (Lepidoptera), while we hypothesise that birds will differ in their response to climate, and so they were analysed separately.

For each macro-moth and butterfly species, we obtained national indices of abundance in two steps: first, for each species, we related the species' annual count data per site to year (as a fixed factor) in a generalised mixed effects model with site as a random intercept, and a Poisson error distribution. We

then took the fixed (year) coefficients from each species' model, which quantify the relative abundance of species each year.

We calculated year-to-year changes in the index by subtracting the \log_{10} index value in year_t from the \log_{10} index value in year_{t+1} (Figure 1C-D). We also calculated each species' long-term change in abundance over the four decades of our study period as the slope of a linear model relating national indices of abundance against year.

(b) Climate data

We downloaded gridded climate data for the period 1965–2011 from the UK Met Office website (www.metoffice.gov.uk/climatechange/science/monitoring/ukcp09); supplemented with data for 2012 obtained directly from the Met Office. These data provide daily estimates of minimum and maximum temperature, and monthly rainfall estimates, at a spatial resolution of 5 km × 5 km on the Ordnance Survey National Grid reference system. From these data, we derived a set of 13 annual climate variables that may correlate either directly (physiological limits) or indirectly (i.e. relevance for habitat, food or host plants) with the population dynamics of our study species (Supplementary Tables 1 and 2). Further analyses were conducted on spatial mean values, calculated across England, for each year in the population time series.

We reduced levels of collinearity in the climate data using the following procedure, whereby highly correlated variables (Pearson's $|r| > 0.7$) were sequentially removed. For each pair of correlated variables in turn, starting with the most strongly correlated pair, the variable that was collinear with the greatest number of other climate variables was removed; where a pair of variables was collinear with the same number of other variables, the one with the largest mean absolute correlation was removed. The seven retained climate variables included measures of rainfall seasonality, drought, temperature range, growing degree days as well as coolness and hotness (Table 1).

We summarised temporal variation in these variables by plotting the first three axes of a principle components analysis, using the 'PCA' function of the 'FactoMineR' package in R (32). For comparison with the species data, we computed the 3-dimensional Euclidian distance of each year from the origin of the PCA, which is a measure of how unusual a year was in terms of the unique combinations of climate in that year.

(c) Statistical analyses

Defining and describing extreme events

There are many different approaches to defining an extreme event, including identifying observations at the tails of a given frequency distribution (typically, and arbitrarily, selecting 5 or 10% of the data), or those above or below an absolute critical threshold (see e.g. 22, 23, 33, 34, 35). In the context of our study species, the percentile approach would mean all species would be assigned at least one good year and one bad year, irrespective of the spread of year-to-year changes in index across their study periods. We therefore identified extreme changes as those beyond species-specific thresholds, defined by the median value over the study period \pm two median absolute deviations (MAD) (36), according to Equation 1:

$$\{|x_t - \text{median}(x)| / \text{MAD}\} > 2 \qquad \text{Equation 1}$$

where x_t is a species' year-to-year change in index in year t , and x is the full time series of the species' year-to-year changes in index. Thus, we defined explosions and crashes relative to the median in a symmetrical fashion (see e.g. Figure 1), because we found no consistent asymmetries in species' changes in index (robust measure of skewness (37): mean across all species = -0.02 [range, -0.47 to 0.44]). We used this same approach to define extreme climate years, according to the seven climate variables in Table 1.

We investigated the degree of association between the occurrences of explosions / crashes across all years by correlating the proportion of Lepidoptera (or birds) experiencing population crashes each year to the proportion of Lepidoptera (or birds) experiencing population explosions, using Spearman's rank correlations. We then identified 'consensus' years, during which more species experienced extremes in the same direction (crash or explosion) than would have been expected by chance, based on a one-tailed exact binomial test using the observed frequencies of crashes and explosions within each group (Lepidoptera or birds, with Bonferroni correction for multiple-year testing).

To investigate whether population trends were related to extreme population responses, each species' long-term change in abundance was plotted against the maximum absolute population crash or explosion (that qualified as an extreme) for that species, and also against the mean of all extreme crash or explosion events experienced by that species during the study period. These two metrics

should reveal whether extreme population changes have a long-term effect on population size (e.g., if numbers were high and crashed in year 5, and stayed low thereafter, there would be a negative relationship between year and population size; but if there was density-dependent recovery, there would be no relationship, or even a positive relationship). Species that did not show any extreme population change values ($n = 2$ birds, 27 moths and 3 butterflies) were excluded from this analysis.

Linking population extremes to climate

Each period of population change refers to the change in index values (counts) between years, for example between 1968 and 1969. Each climatic year also corresponds to a 12-month period (with the exception of drought index), such that the climate referred to as ‘1969’ refers to the climatic period from September 1 1968 to August 31 1969 (see Table 1). The data for these two years would be compared to consider direct (lag 0) effects of climate on population change (e.g. the 1969 climate compared to the 1968-1969 population change). Population crashes and explosions were also related to climatic conditions in the previous year (climatic year ‘1968’, lag 1). We considered lagged effects because impacts of ECEs can be direct (e.g., population growth in response to a warm summer), or delayed by a year or more due to species’ long generation times or through altered natural enemy or food abundances.

First, we investigated whether consensus years corresponded to extreme climate years, as defined in Table 1. Then, in order to investigate more generally if extreme population responses were associated with ECEs, the summed number of Lepidoptera or bird species experiencing an extreme event (crash or explosion) each year was plotted against (i) the 3-dimensional Euclidian distance from the PCA origin, (ii) drought index and (iii) daily minimum temperature of coldest 30 days, as we hypothesised these would be the main drivers of population change for our focal species groups. In each case we accounted for a direct and a lagged effect. As such, statistical inference was Bonferroni-corrected for multiple ($n = 12$) tests.

Results

(a) Extreme population changes

At least three extreme population changes took place in every year, revealing that every year in our four-decade study period was unusual from the perspective of some species (Figure 2A-B). The majority of species experienced at least one extreme population change during their study periods: 86% of Lepidoptera (177 out of 207 species), and 93% of birds (29 of 31).

We detected a significant negative association between the proportion of Lepidoptera experiencing population crashes and the proportion experiencing population explosions across years (Spearman's rank correlation: $S = 22284.09$, $r_s = -0.57$, $p < 0.0001$), indicating that when multiple species did exhibit extreme changes in the same year, they tended to respond in the same direction. This was not significant for birds ($S = 13689.1$, $r_s = -0.11$, $p = 0.49$). Extreme population changes were, nonetheless, expressed in different directions in 41 of the 44 years considered (i.e. the populations of some species crashed and others exploded in the same year). Furthermore, even in the most extreme years (see below), most species did not exhibit extreme population responses, demonstrating the individualistic nature of the extreme population changes exhibited by species.

Out of a possible 10,178 species-by-year combinations, 374 (3.7%) population crashes and 257 (2.5%) population explosions were detected: an excess of crashes over explosions (two-tailed exact binomial test, $n = 631$, $p < 0.001$). Crashes also tended to be larger in their absolute magnitudes than explosions in both Lepidoptera (Welch two-sample t-test: $t = -3.82$, d.f. = 454.05, $p < 0.001$) and birds ($t = -2.41$, d.f. = 116.71, $p < 0.02$). For Lepidoptera, crashes (mean = -0.52, range -1.03 to -0.22) were on average around 13% greater in magnitude than explosions (mean = 0.46, range 0.21 to 1.30). Similarly for birds, crashes (mean = -0.13, range -0.48 to -0.03) were on average 18% greater in magnitude than explosions (mean = 0.11, range 0.04 to 0.23).

The numbers of extreme population changes in a given year for moths were strongly positively correlated with the numbers of extreme population changes in the same year for butterflies (Spearman's correlation: $S = 3098.72$, $r_s = 0.60$, $p < 0.0002$; Figure 2C), suggesting that common external drivers were responsible for population crashes and explosions in Lepidoptera. However, comparing Lepidoptera and birds revealed a negative correlation ($S = 16433.1$, $r_s = -0.33$, $p = 0.03$; Figure 2D), suggesting that birds and Lepidoptera are responding to different external drivers, or to similar events but with different lagged responses.

The existence of common drivers that acted across multiple species was supported by the detection of five ‘consensus’ years for Lepidoptera (1975/76, 1976/77, 1992/93, 2006/07, and 2011/12) during which statistically-unusual numbers of species showed population explosions or crashes (at $p < 0.05$, after Bonferroni correction). Only one of these (1975/76) was a consensus good year, while the other consensus years were bad years, during which nearly all extreme population changes (54 out of 59 in 1976/77, 25 out of 26 in 1992/93, 30 out of 32 in 2006/07 and 42 out of 42 in 2011/12) were negative (Figure 2A). However, even during their largest consensus years, only 26% of Lepidoptera species and 32% of bird species experienced extreme population responses.

In contrast, for birds, only one consensus year was detected (1981/82) as statistically significant ($p < 0.05$, after Bonferroni correction; 1990/91 was significant prior to correction), during which ten of the 31 species crashed (Figure 2B). The lower numbers of bird species compared with Lepidoptera in our analyses (31 rather than 207 species) may explain this apparent difference between taxa, and so it should not be deduced that birds necessarily experienced fewer consensus years than Lepidoptera.

(b) Associations between biological and climatic extremes

Five of the six consensus years for extreme population change coincided with one of the extreme climate years, either directly ($n = 3$) or with a one-year lag, which is consistent with the hypothesis that there is a positive association between population consensus years and extreme climatic conditions (Fisher's Exact-Boschloo test, one-sided $p = 0.015$). The sixth consensus year for population change (1992/93), which was the smallest of the consensus population crashes (Figure 2), was not associated with any climatic extremes (Table 1).

In the only consensus year for birds (1981/82), 32% (10 of 31 species) of species crashed during exceptionally cold winter weather in that year (Table 1; Figures 2 and 3). In 2006/07, the large consensus year for Lepidoptera coincided with high growing degree days in that year, as well as an extremely summer in the previous year (i.e. 2005/06; Table 1; Figures 2 and 3). The large number of Lepidoptera crashing in 2011/12 followed an extreme cold in the previous winter.

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294 The one consensus good year for populations was 1975/76, when 9% ($n = 16$) of moths were
295 positively affected (butterflies could not be considered because data collection did not start until the
296 following year). The climate in 1975 was relatively dry, with the summer of 1976 being extremely
297 hot and dry (Table 1, Figure 3C-D) with a drought index nearly double the median over the study
298 period (Figures 2A, 3D, Table 1). Subsequently, significant numbers of Lepidoptera (54 of 207
299 species, 26%) experienced population crashes between 1976 and 1977. However, while 1976/77 was
300 the largest consensus year for Lepidopteran crashes, a few Lepidoptera (4 of 207 species)
301 experienced population explosions in the same year. This suggests that there can be cumulative
302 effects, and that some climatic extremes may generate opposite direct and lagged effects (in this case,
303 increase followed by crash).

304

305 Five of the ten climatically-extreme years did not coincide, with or without lag, with any of the
306 consensus population change years in either Lepidoptera or birds. Given that extreme events tended
307 to happen in different years for Lepidoptera and birds (Figure 2D), it is possible that other taxa
308 responded strongly in these years. The pattern of apparently mixed responses is also exhibited by
309 individual species. For example, the mottled grey moth *Colostygia multistrigaria* population crashed
310 after the 1976 drought, but not after other dry years, and the tree sparrow *Passer montanus* declined
311 in association with some, but not all, cold winters (Figure 1).

312

313 We then considered extreme population changes in all years in relation to PCA scores, drought and
314 winter cold. There was no correlation between 3D distance from the PCA origin (a measure of how
315 climatically-unusual a year was) and the proportion of species experiencing an extreme event (Figure
316 4). The relationships between species' responses, drought and winter cold were also noisy for both
317 Lepidoptera and birds (Figure 4), with only two significant relationships detected after Bonferroni
318 correction. The first significant relationship was for drought index of the previous year and the
319 proportion of Lepidoptera species experiencing an extreme change ($t_{41} = 3.30$, $r = 0.48$, $p = 0.002$;
320 Figure 4D). The second was a significant negative correlation between the proportion of birds
321 experiencing an extreme population change and daily minimum temperature of the coldest 30 days
322 ($t_{39} = -3.48$, $r = -0.49$, $p = 0.001$; Figure 4E). However, in both cases, the correlations ceased to be
323 significant (after Bonferroni correction) once the largest consensus year was removed (1976/77 for
324 Lepidoptera, $t_{40} = 1.45$, $r = 0.22$, $p = 0.15$; 1981/82 for birds, $t_{38} = -2.81$, $r = -0.41$, $p = 0.01$). This
325 reinforces the view that consensus years are genuinely unusual. In the analyses above we reported the
326 proportion of species experiencing an extreme change (both explosion and crash), but results were

qualitatively the same when analysing those experiencing crashes or explosions, separately (see Supplementary Figures 1 and 2, respectively).

(c) Extremes and long-term population trends

Overall, there was little relationship between the extreme population changes that a species exhibited and species' long-term population trends (Figure 5). Extreme population events are modest predictors of long-term trends, at best, and for the Lepidoptera in our study may not be linked at all.

For Lepidoptera, we first compared two groups of species: those for which the single most extreme event was a crash, and those for which the single most extreme event was a population explosion. We found no association between extreme population change and trend (one-tailed Wilcoxon rank sum test: $W = 3439.5$, $p = 0.19$; Figure 5A). We then took the mean of all extreme events exhibited by each species. Again, there was no difference between the long-term population trends of 'crashing' and 'exploding' species ($W = 3583$, $p = 0.45$; Figure 5C). Regardless of the direction and magnitude of the extreme, some species showed long-term increases, and others showed long-term declines.

When we repeated this analysis for birds, we did find an effect of extreme events. We found that bird species experiencing population explosions (as single events, or the mean of their species-specific extremes) tended to have more positive long-term population trends than bird species that exhibited crashes (for single events, $W = 144.5$, $p = 0.005$ [significant after Bonferroni correction]; average of all extremes, $W = 128.5$, $p = 0.02$ [n.s. after Bonferroni correction]; Figure 5). As in the Lepidoptera, some crashing bird species showed long-term population increases and others decreases. The different results for Lepidoptera and birds suggest that there may be taxonomic differences (perhaps linked to generation times) in the association between extreme events and long-term trends.

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3. Discussion

(a) The frequencies and magnitudes of extreme population events

Extreme population responses were observed in all years, and in at least one year for the majority of species: moths, butterflies and birds. Furthermore, in the majority of years, one or more species showed extreme positive population growth (explosions) while others showed rapid declines (crashes). These findings show that extreme population changes are individualistic among species; an extreme event for one species is not necessarily an extreme event for another. Individualism can be expressed not only in the particular climate variables (or other drivers) that a species responds to, but also in the time delays between an event and the population response. The observed effects can be direct (e.g., population growth within a warm year), delayed by a year (e.g., drought-induced mortality of Lepidoptera that is not recorded until adults fail to emerge the next year), or delayed by two or more years via community interactions (e.g., through altered natural enemy or food abundances) (38). Delayed density dependence (population crash following a ‘good’ year, or vice versa) may add further lags to the system. Across all 238 species, a combination of delayed community and density-dependent effects could mean that extreme population responses are more evenly spread across years than the ECEs that may trigger these changes. The longer generation times, larger body size, higher trophic level (on average) and homeothermic biology of birds, compared to Lepidoptera, may tend to spread their observed responses more evenly across the years, as we observed. The (weak) negative correlation between the responses of birds and Lepidoptera (Figure 2D) may stem from different lag times, differences in which aspects of environmental variation they respond to, and different overall sensitivities to the climate.

Although species were generally individualistic in their responses to extreme events, there was some agreement across species. First, there was evidence that species groups as a whole tended to respond in the same direction in a given year (i.e. experiencing either crashes or explosions), presumably in response to the same (climatic) drivers. Second, we detected six ‘consensus years’ in which a statistically-significant excess of species exhibited crashes or population explosions. Furthermore, each of these years was characterised by near unanimity in the direction of the extreme population response. Although we should be cautious in interpreting five consensus bad years to one consensus good year as an excess of negative extreme events, we also found significantly more (by 46%) crashes than population explosions across the entire data set. These observations are consistent with the hypothesis that more bad than good events are expected when the climate is changing rapidly. If populations show some degree of local adaptation to historical conditions, they may show extreme

population collapses under novel conditions (even if they subsequently recover through adaptation to the new conditions).

There was also a tendency for the magnitudes of crashes to be greater than the magnitudes of increases. We interpret this as arising because it is, in principle, possible for all individuals within a large population to die simultaneously when they experience an extreme event, whereas population growth is constrained by the intrinsic rate of increase of a species. Nonetheless, for insects, the potential fecundity of individuals is high, and so extreme population growth can occasionally be achieved, especially for species that can accomplish multiple generations within a single year.

Overall, we conclude that a few species exhibit extreme population changes in most years, and that most species show extreme population changes in some years, but that there are some years that are characterised by excesses of dramatic population changes. Furthermore, there is an excess of population crashes, relative to explosions and there is a tendency for crashes to be larger in magnitude than increases.

(b) The link to climate

Linking all of these extreme population changes to variation in the climate is difficult, given that extreme population responses took place in every year and lagged responses can occur. Moreover, some population explosions and crashes may have nothing to do with the climate, or with the interaction between the climate and other species. Biological interactions that take place within communities, including exaggerated (over-compensating) responses to density-dependent interactions, can potentially generate population fluctuations in the absence of external drivers.

However, there are several lines of evidence that lead us to suggest that the majority of the rapid changes observed here do stem from a geographically-widespread external driver, with climate the most likely candidate. First, the year-to-year population crashes and explosions that we detected took place at a national-scale (England). These are unlikely to be driven by more local factors, such as local habitat change, or local interactions between species that are unrelated to a widespread driver. Second, we found a strong positive correlation between the responses of our two groups of Lepidoptera (butterflies and moths) across years (Figure 2C), and a negative correlation between Lepidoptera and birds (Figure 2D). Given that the recording schemes for these three groups are independent, these correlations imply responses to climate events that are both geographically

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4 420 widespread and capable of generating between-year changes. Thirdly, the existence of statistically-
5 421 significant consensus years (and agreement on whether these years are good or bad) again implies
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7 422 that some relatively fast-acting underlying causation is operating at the geographic scale of the whole
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9 423 of England. Changes in land use and habitat management (which affect micro-climate), pesticides,
10 424 the arrival of invasive species, and other drivers that contribute to longer-term trends are unlikely to
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12 425 act so broadly in a single year; it is only their interactions with widespread climatic factors that are
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14 426 likely to drive such effects (39). We conclude that most (but not all) of the extreme population
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16 427 crashes and explosions that we have detected stem directly or indirectly from a near-synchronous,
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18 428 geographically widespread process, which is most likely to be the climate.
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20 430 In general, we demonstrated an overall lack of association between climate and population responses
21 431 across all years. However, we did find that consensus years (when many species showed extreme
22 432 changes) were more likely to occur in years that were also extreme from a climatic perspective. With
23 433 such rare events (six consensus years), we should be cautious about attributing them to specific
24 434 climatic conditions. Nonetheless, five of the six consensus years, appear to be associated with either
25 435 cold winters (historic extremes that may be becoming less frequent and extreme), and with hot and
26 436 dry summers (extremes that may increase in frequency and strength). Similarly, when we looked
27 437 across all extreme responses rather than just the consensus years, we found positive associations with
28 438 drought (for Lepidoptera) and winter cold (for birds). It should be noted that there were some years
29 439 which were climatically extreme but did not generate biological consensus years; but given that birds
30 440 and Lepidoptera differed in their dynamics (i.e., responding most strongly in different years) it is
31 441 entirely feasible that other taxa that we did not study responded strongly in those years.
32 442
33
34 443 Three of the six biological consensus years took place in the same year as a climatic extreme, but the
35 444 negative effects of hot and dry conditions in 1976, and of extreme winter cold in 2010/11, were
36 445 mainly observed as lagged population responses (around a quarter of the Lepidoptera species crashed
37 446 in 1976/77). The summer of 1976 was hot, and also experienced the greatest drought index in the 45-
38 447 year time series, owing to hot and dry conditions stretching back to the spring/summer of 1975
39 448 (Figure 1). This apparent lag in Lepidoptera response may be an issue of detection rather than a true
40 449 biological phenomenon; individuals may have died in the summer of 1976, but it was not until the
41 450 1977 generation failed to emerge that this was noticed. For example, numbers of the Adonis blue
42 451 butterfly *Polyommatus bellargus* crashed after its hostplant *Hippocrepis comosa* dried up and
43 452 caterpillars then starved (40); and other species with summer-feeding larvae were also negatively
44 453 affected (41). The ringlet butterfly *Aphantopus hyperantus* also crashed (42) and so it seems likely

that direct effects of the 1976 drought were largely responsible for the subsequent population crashes of other Lepidoptera. Impacts of summer drought conditions upon birds are likely to be weaker than for Lepidoptera (bird populations did not change abnormally in 1975/76 or 1976/77), although there is some previously-documented evidence for lagged effects on some bird species that feed on soil-invertebrates (e.g. 38) as well as on those that are migrants (10).

(c) Are population trends determined by extreme events?

It would seem reasonable to suppose that populations exhibiting major crashes would tend to decline in the long term, and those experiencing population explosions would increase. However, extreme events are rare, and many smaller population changes in ‘normal’ years might fully compensate for such extreme events. Density-dependent responses to extremes may also prevent any long-term consequences of extreme events from being realised. Our data suggest that any impact of single extreme events on long-term trends is limited (Figure 5). In particular, for Lepidoptera and bird species experiencing population crashes (either as the most extreme event they experienced or as the average of all extreme events), some of them showed long-term declines and others showed long-term increases. The same was true for Lepidoptera that experienced population explosions. It was only in birds where species explosions tended to be linked to more positive long-term population trends.

There is no universal ‘best way’ to test for the effects of extremes on long-term trends, but we urge others to test rather than assume that the two will be linked. Weak associations are not particularly surprising. Only 6.2% of all between-year population changes qualified as extreme, and hence the magnitude of extreme events would have to be far greater than regular population changes for such events to leave a strong signature on the overall population trend. Reducing the threshold for detecting ‘extremes’ (so there are many more of them) might increase the likelihood of detecting an association, but this would be counter to the notion that extreme events are, by definition, unusual. Altwegg et al. (this issue) report that observational studies of the impacts of extreme climatic events have tended to investigate one extreme event during a median study duration of 11 years, which is comparable to the frequency of extreme population responses identified here. Of course, single events that reduce population densities by two or more orders of magnitude can happen (18, 26), but they are very rare when considering the number of between-year population changes that we studied. Long-term population trends are seemingly dominated by other factors, such as relatively gradual climatic changes, or by non-climatic events that accumulate over space and time. For example, many

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4 488 farmland birds showed declining trends during the 1970s and 1980s as a result of agricultural
5 489 intensification operating over many years (43, 44). Similarly, land-use change is the likely driver of
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7 490 the parallel long-term declines of many Lepidoptera species in the United Kingdom (45, 46). In no
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9 491 single year would there be sufficient intensification to cause a detectable crash at a national scale, but
10 492 the accumulation of local effects over many years seems to drive the long-term trend. Other factors
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12 493 such as the arrival of invasive species or other locally-acting pressures can have similar effects
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14 494 provided they operate for long enough; multiplicative effects of climatic and non-climatic factors
15 495 may also be important (39).
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19 497 An additional reason why a link between extreme population events and long-term trends may not be
20 498 apparent could be related to historical extreme events (constraints) that are no longer in operation.
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22 499 Climate warming may be just as likely to reduce or remove some historical constraints as to impose
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24 500 new ones. For example, the insectivorous Dartford warbler *Sylvia undata* was virtually extinguished
25 501 from England by the severe winter conditions of 1961/62 (47), but this bird species has subsequently
26 502 increased in abundance and expanded its distribution in the absence of such a severe winter cold
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28 503 constraint (14). Dartford warblers still do worse in cold winters, but these temperatures are now
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30 504 insufficiently cold to determine the overall population trend. This phenomenon would lead to little or
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32 505 no correlation across species in their most extreme population responses and their overall population
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34 506 trends. Species may be released from historical constraints (including extremes), just as they may be
35 507 hampered by novel ones.
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39 509 **4. Conclusion**

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41 510 In every year of our 45 year time series, at least three species of Lepidoptera and/or birds showed an
42 511 extreme response in population size, giving support to our first hypothesis, that the responses of
43 512 species to climatic variability are individualistic. We also found support for our second hypothesis:
44 513 population crashes tended to be more frequent than population explosions during periods of rapid
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46 514 climatic change (as new conditions are experienced by populations that are potentially locally-
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48 515 adapted to historical conditions). Furthermore, population crashes were more extreme than
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50 516 explosions (explosions are constrained by the intrinsic rate of population growth whereas it is
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52 517 possible for all individuals to die). Thirdly, we did find that there were statistically-unusual
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54 518 consensus years when many species experienced population crashes or explosions, and we obtained
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56 519 support for the hypothesis that these events were associated with climatically extreme years. Finally,
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58 520 we found only limited and weak support (among birds) for the hypothesis that long-term population
59 521 trends are correlated with extreme population responses, probably because the processes that are
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4 522 operating in most years (which are not extreme) are usually more important determinants of long-
5 523 term trends than are rare extremes. We conclude that extreme population events are individualistic
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7 524 despite occasional consensus years, and likely to be linked to climatic extremes (from the perspective
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9 525 of each species), but that these extreme events are only weak predictors of long-term population
10 526 trends for the taxa we consider.
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For Review Only

Additional Information

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Data Accessibility

The raw data for these analyses are available from the organisations listed in the acknowledgements. Bird data are available via: www.bto.org/research-data-services/data-services/data-request-system, and butterfly data via: www.ukbms.org/Obtaining.aspx.

Author Contributions

C.D.T. conceived, and C.D.T., G.P., C.D., P.J.P. and J.K.H. designed the study. J.W.P-H, J.W.C., T.B., D. B.R, and R.F. provided data, with additional assistance from Dario Massimino, while G.P. and P.J.P. carried out the analyses. C.D.T., P.J.P. J.K.H. and G.P. drafted the manuscript, and all authors contributed to revising the paper. All authors gave final approval for publication.

Competing Interests

We have no competing interests.

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Tables

Table 1. Climate variables used in the analyses. The plus and minus columns identify ‘extreme’ years in which the England-wide average conditions were greater than (+) or less than (-) twice the median absolute deviation from the median. With the exception of the drought index, each variable was calculated over the 12-month period from September 1 to August 31 (i.e., 1979 corresponds to the period September 1st 1978 to August 31st 1979). For the drought index, calculations ran over an 18-month period (beginning March 1) in order to capture water deficit accumulated over successive hot and dry springs/summers.

Variable	Abbreviation	Units	+	-	Description
Rainfall wettest month	<u>WETTEST</u>	mm			Rainfall of the wettest calendar month
Rainfall seasonality	<u>RAINSEASON</u>	mm	1979, 1990, 1995		Rainfall contrast across seasons (48): $\sum s = 1.4 Rs - RT/4 /RT$, where Rs is rainfall in season s, and RT is total annual rainfall
Drought index	<u>DROUGHT</u>	mm	1976, 1996		Accumulated water deficit, where a deficit is defined by monthly Hargreaves PET > monthly rainfall. Months with excess rainfall reduce the deficit, but only up to field capacity. The drought index is the maximum water deficit recorded during spring/summer of the reference year
Growing degree days	<u>GDD5</u>	°C	2007		Annual sum of degrees by which daily mean air temperature exceeds 5 °C
Annual temperature range	<u>TEMPRANGE</u>	°C			Annual maximum air temperature minus annual minimum air temperature
Daily minimum temperature of coldest 30 days	<u>COLD30</u>	°C		1979, 1982, 1986, 2011	Mean of daily minima over coldest consecutive 30-day period
Daily maximum temperature of hottest 30 days	<u>HOT30</u>	°C	1976, 1995, 2006		Mean of daily maxima over hottest consecutive 30-day period

Figures

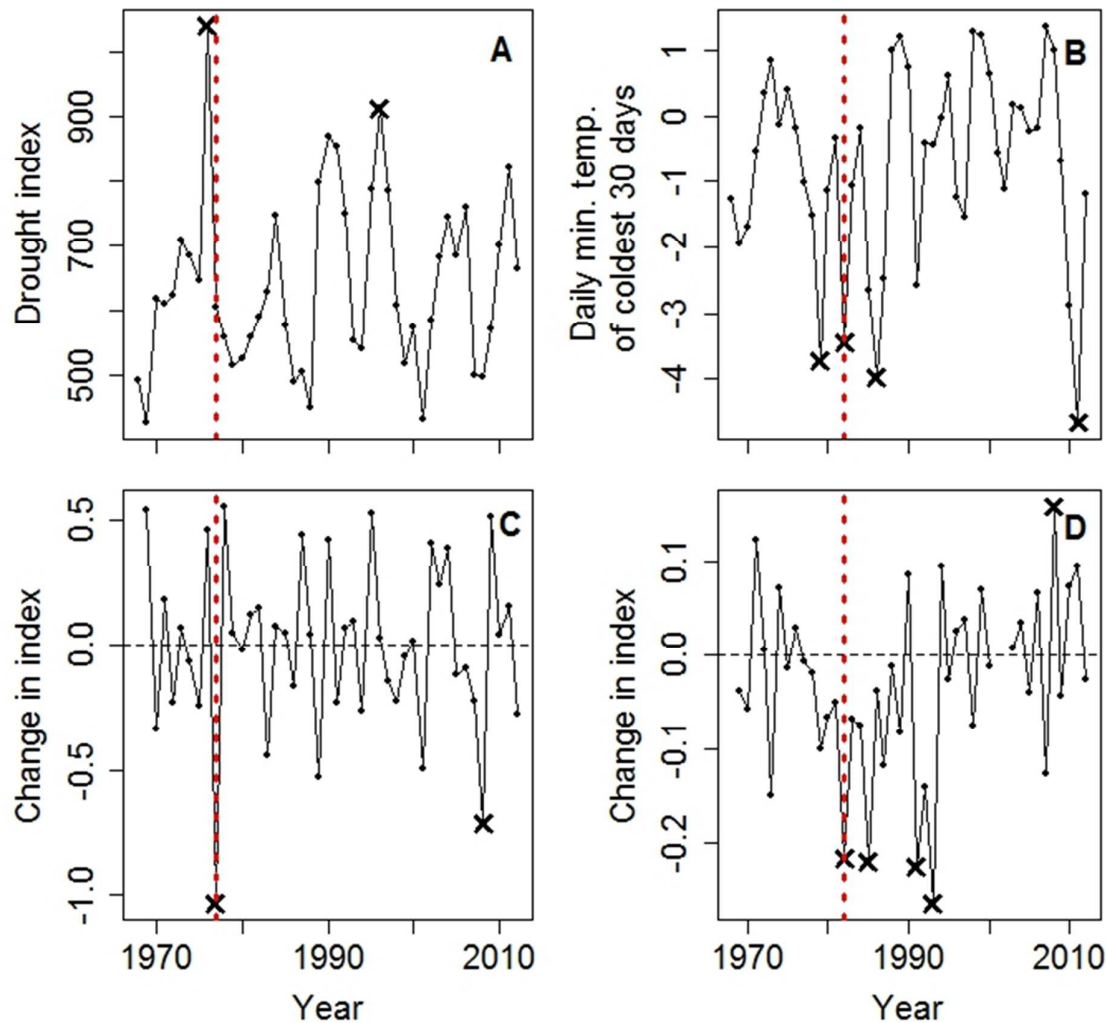


Figure 1. Exemplar climatic variables and species to illustrate our approach. The plots show how we identified extreme climatic events (A and B) and species responses (C and D). The vertical (red) dashed lines represent the largest consensus year, where an extreme number of Lepidoptera (A and C) and birds (B and D) experienced population crashes. Panels C and D represent year-to-year changes in index of two example species, chosen as they experienced the greatest crashes in the largest consensus year for each species' group: in C, the mottled grey moth *Colostygia multistrigaria* and in D, the tree sparrow *Passer montanus*. Values below zero in C and D indicate negative population growth, and values above zero indicate positive growth. In each panel, extreme years (outliers) for climate and species are represented by black crosses.

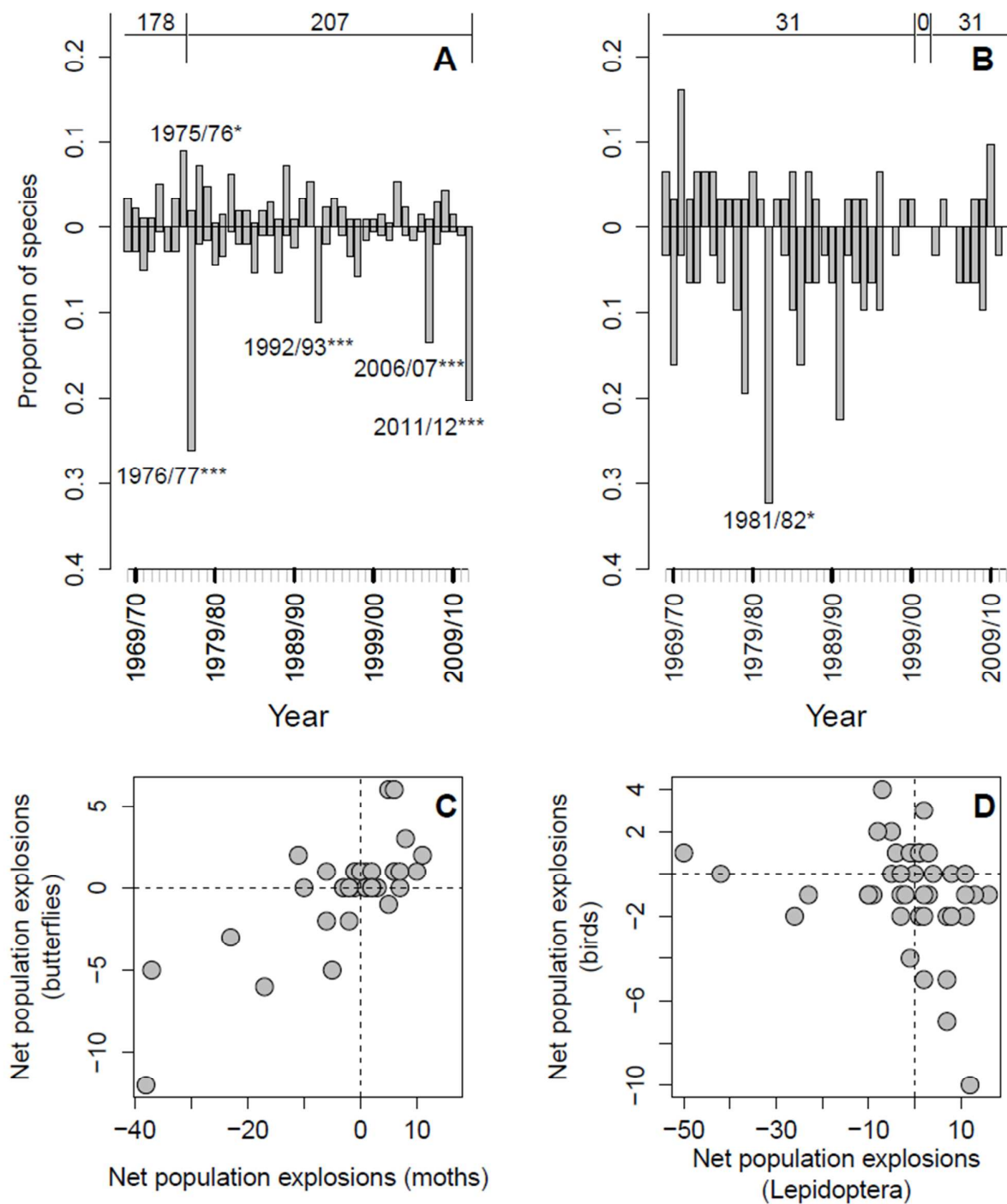


Figure 2. Annual extreme population changes of English Lepidoptera and birds. Upper panels: proportion of Lepidoptera (A; butterflies and macro-moths) and bird species (B) experiencing a population explosion (upwards bars) or crash (downwards bars). Asterisks denote significance of consensus years (*, $p < 0.05$; ***, $p < 0.0001$; Bonferroni-corrected for multiple-year testing); numbers at the top of the plots represent the number of species included in that year. Lower panels: relationships within (C) and between (D) higher taxonomic groups are significant ($p \leq 0.03$). Each filled circle represents one year. ‘Net population explosions’ represents the difference in numbers of species showing population explosions and crashes in a given year (e.g., if there are five species with an explosion and 15 with a crash in the same year, that year scores -10).

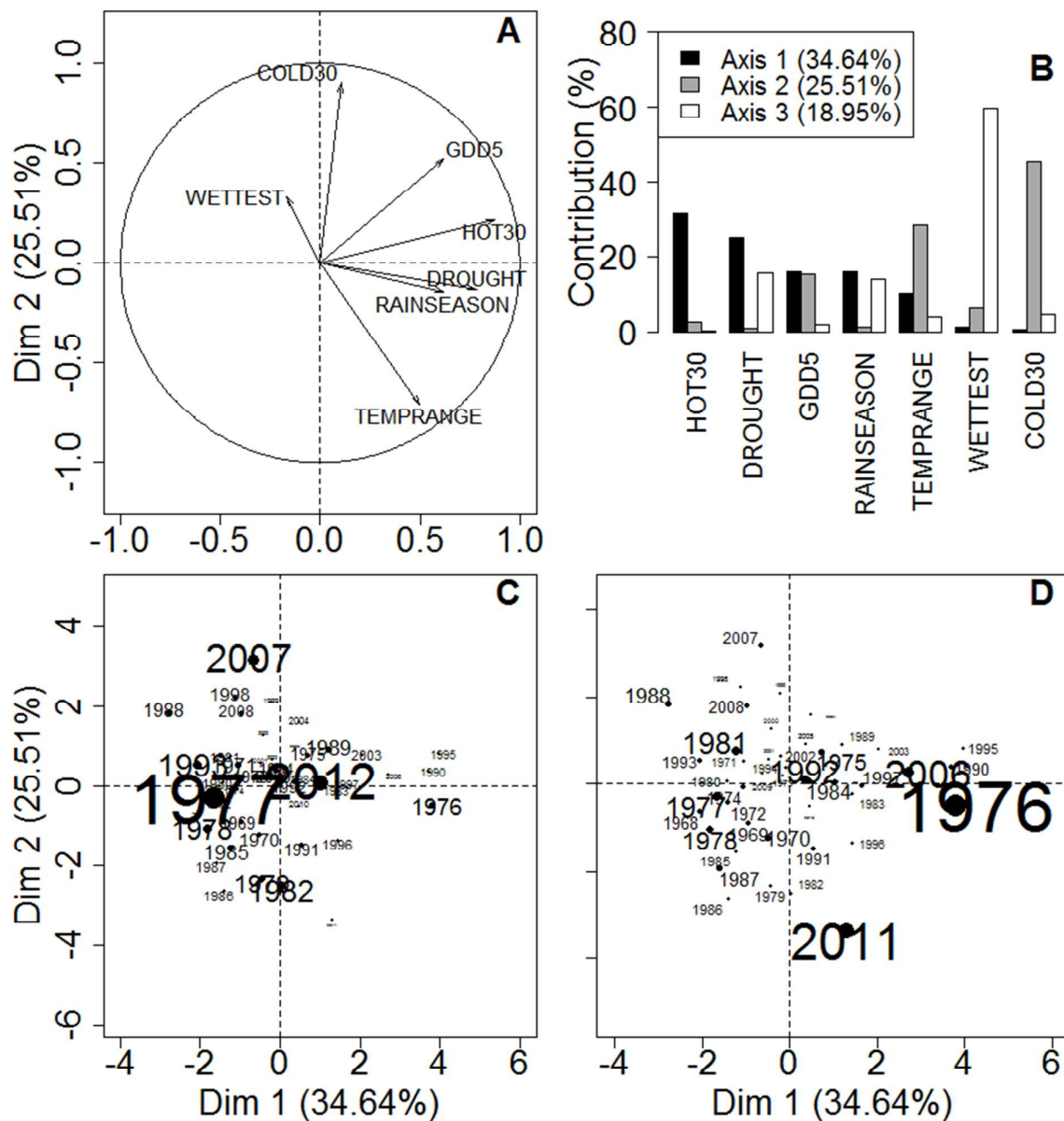


Figure 3. Principal components analysis (PCA) illustrating the variation in the seven climate variables (Table 1) across our study period. Panel A shows vectors for individual climate variables associated with the first two PCA axes (i.e. dimensions, labelled ‘Dim’); Panel B shows the percentage contributions of each variable to the first three PCA axes. Panels C and D show the positions for each year on the first two axes; the size of the text reflects the relative size of the consensus year (i.e. the number of species experiencing an extreme population change) in either the year during which the population change was measured (panel C) or in the previous year (i.e. accounting for a one-year population lag, panel D).

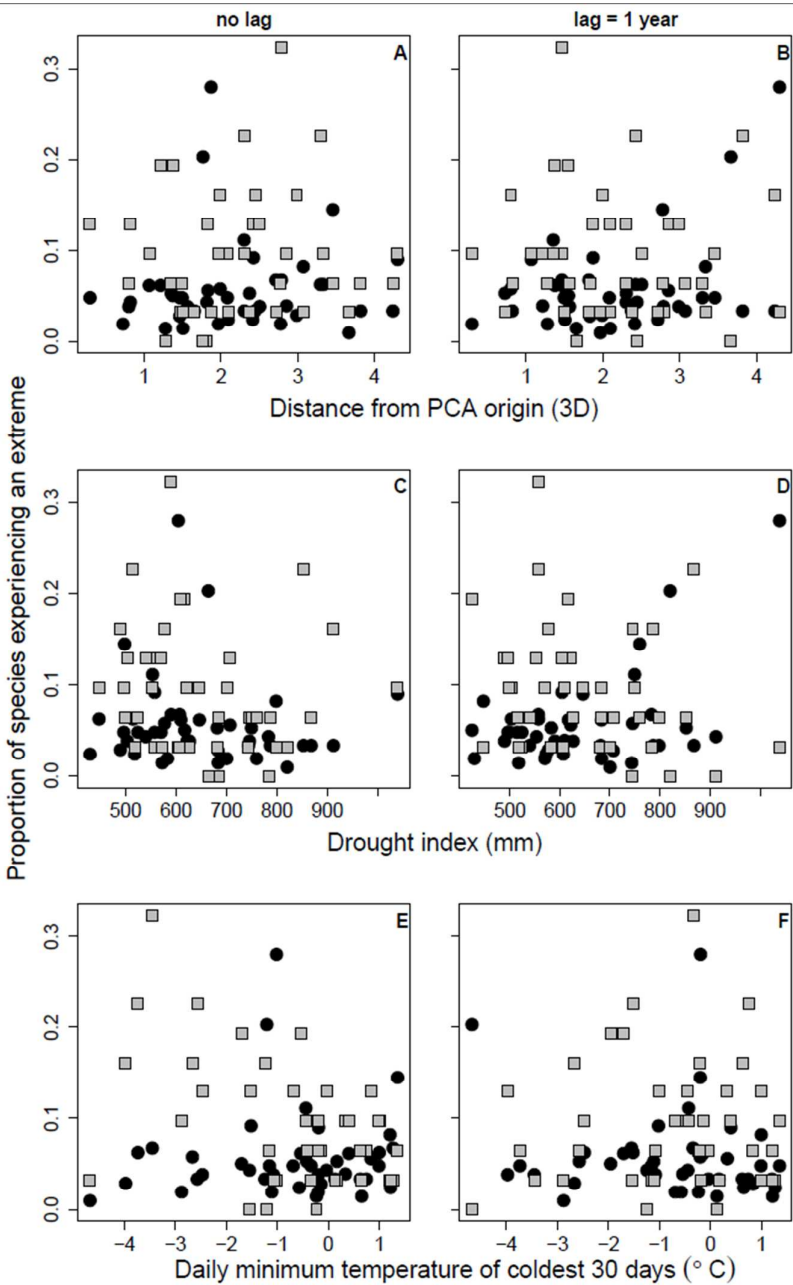


Figure 4. No overall relationship was observed between climatic conditions and the numbers of species showing extreme population responses. Relationships between the proportion of species experiencing an extreme response (either population crashes or explosion) in each year and 3D distance from the climate-PCA origin (A, B), drought index (C, D) and daily minimum temperature of the coldest 30 days (E, F) are shown. Lepidoptera are represented by black circles and birds by grey squares; each symbol represents one year. The lags are measured in years, with lag 0 representing the climate measured in the current year i.e. population changes from 1968 – 1969 were related to the climate in 1968 (lag = 1 year) and/or 1969 (no lag).

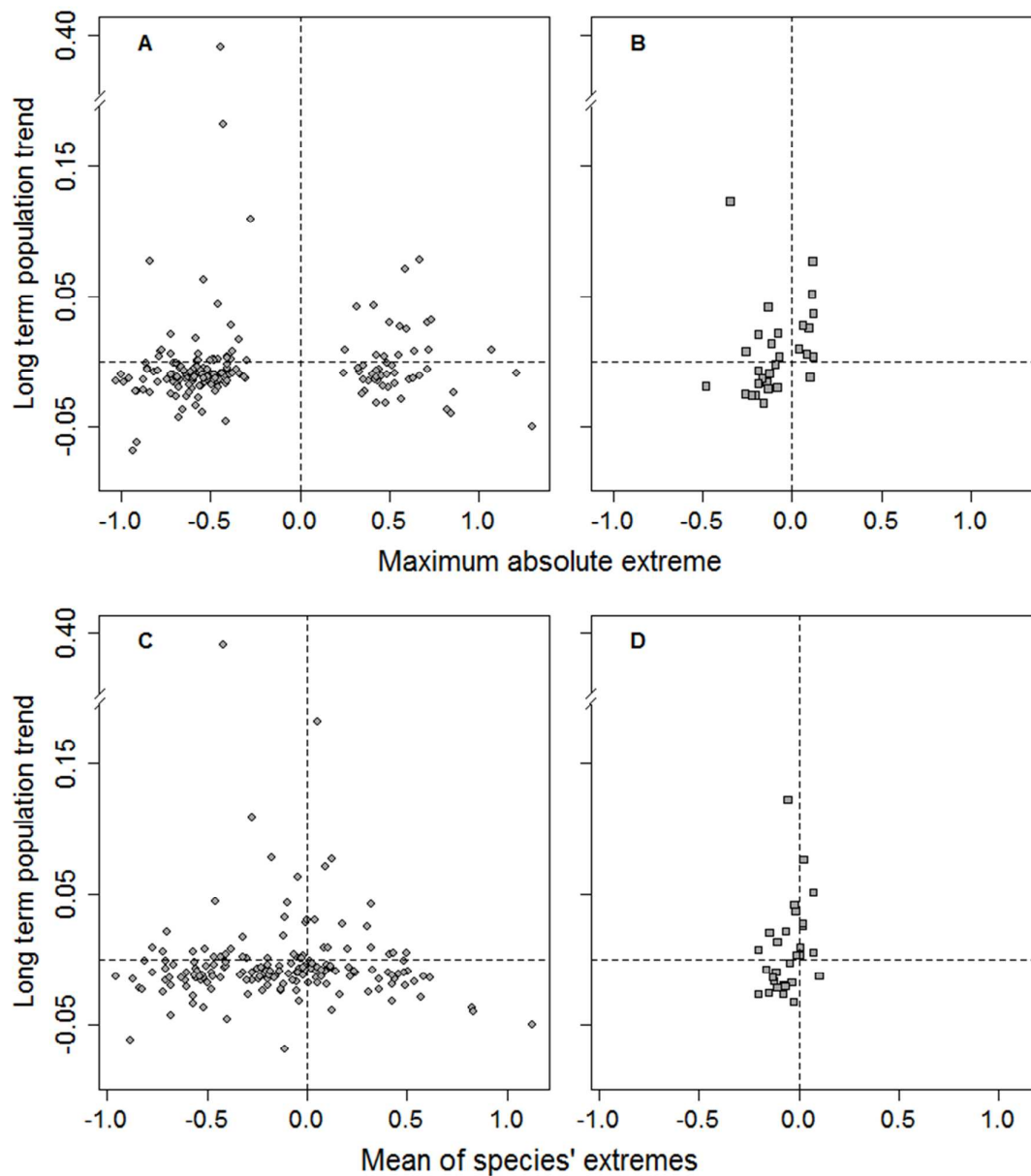
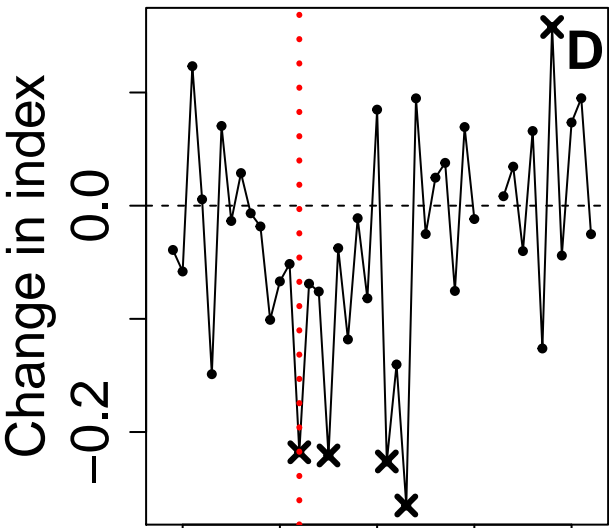
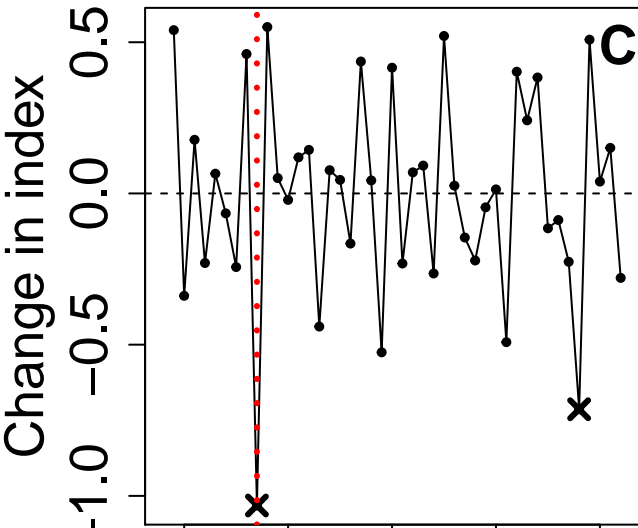
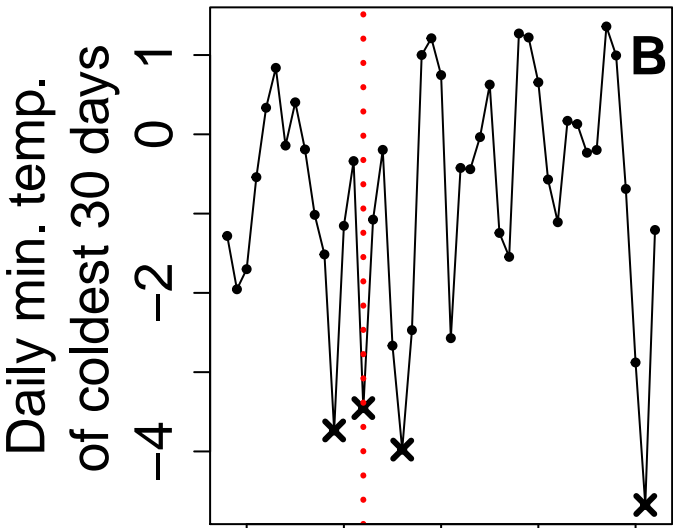
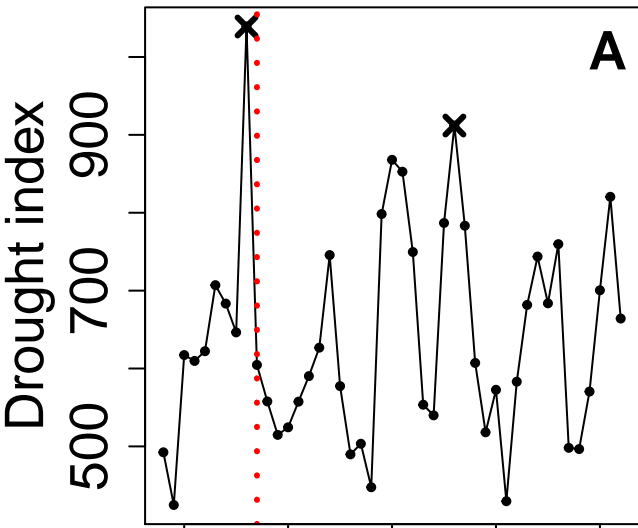


Figure 5. Relationships between Lepidoptera (A and C) and bird (B and D) species' long-term abundance trend and: the maximum absolute extreme value for a species during the study period (panels A and B) and mean over all extreme events experienced by that species during the study period (panels C and D). Note the broken y-axes.

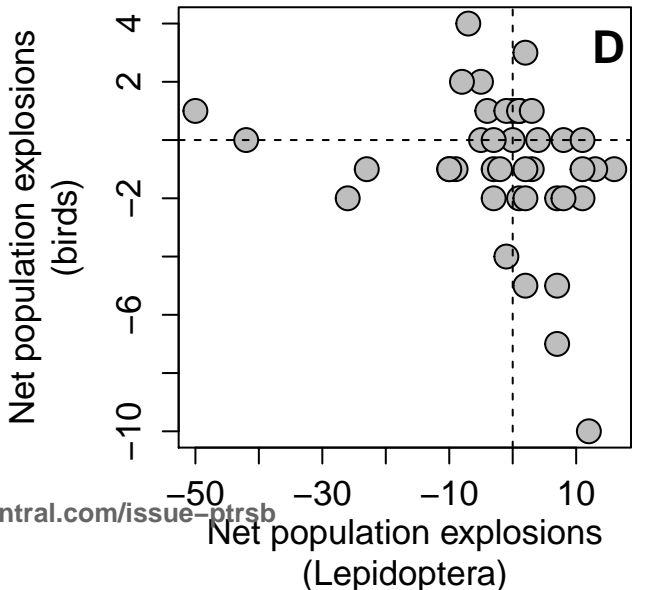
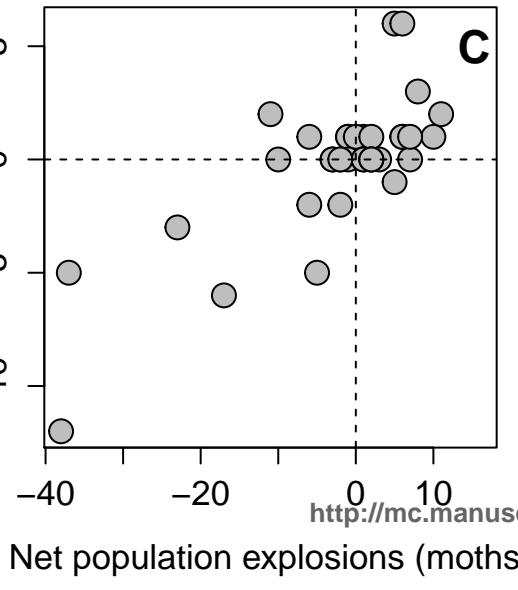
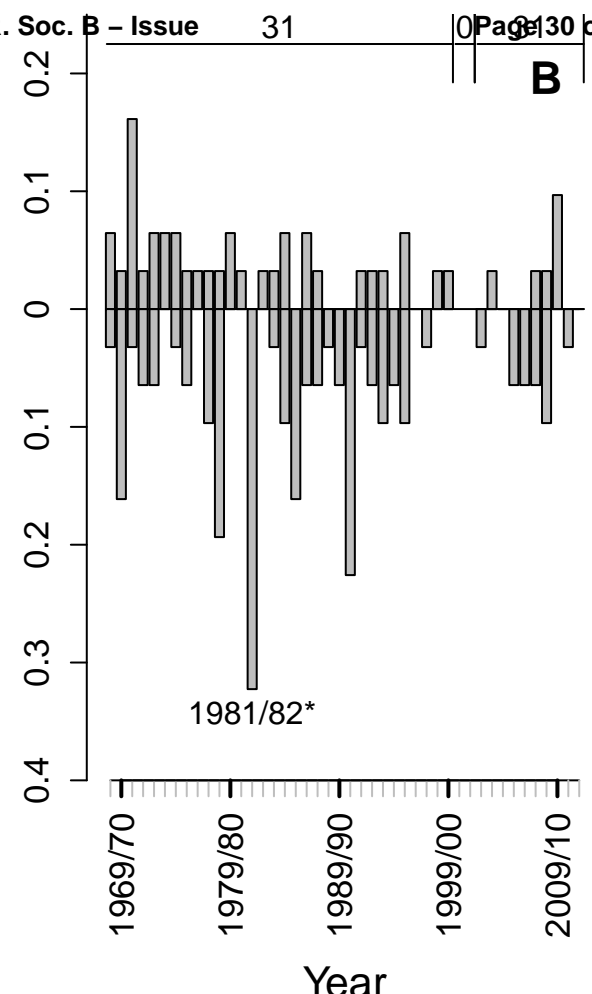
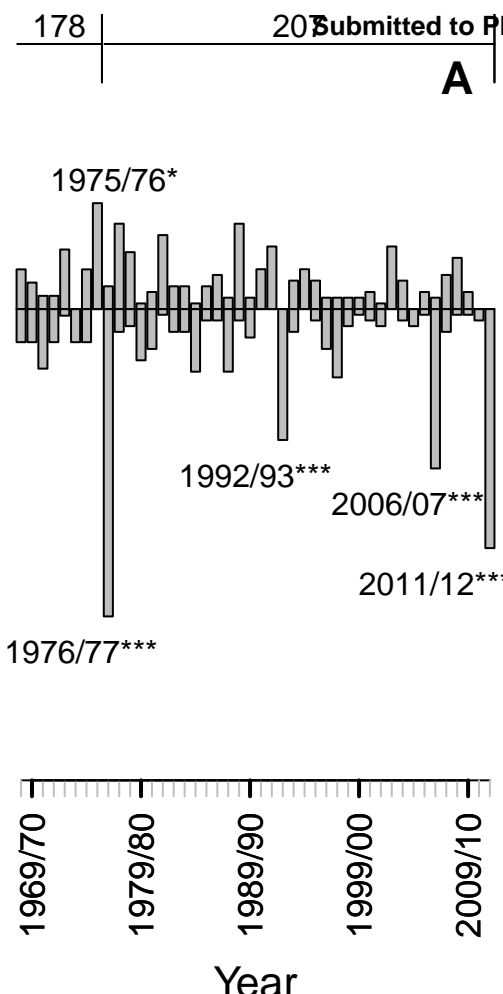


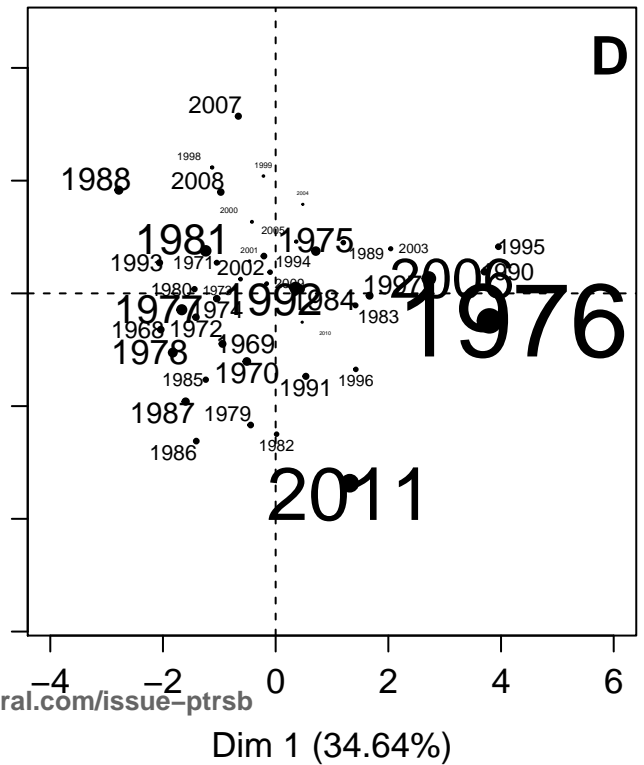
1970 1980 1990 2000 2010

Year

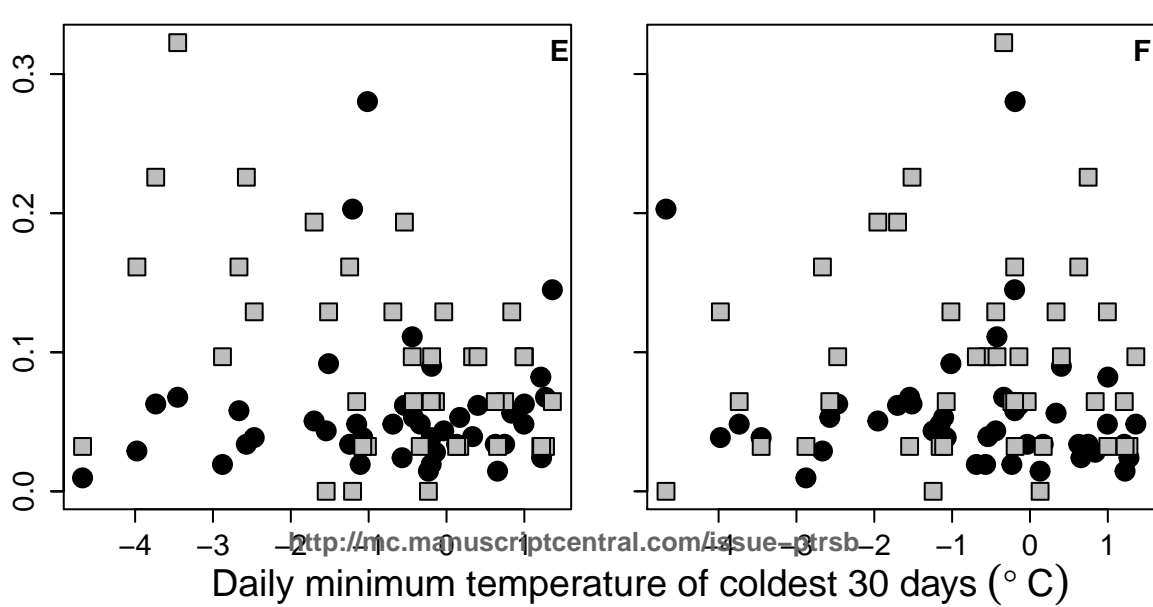
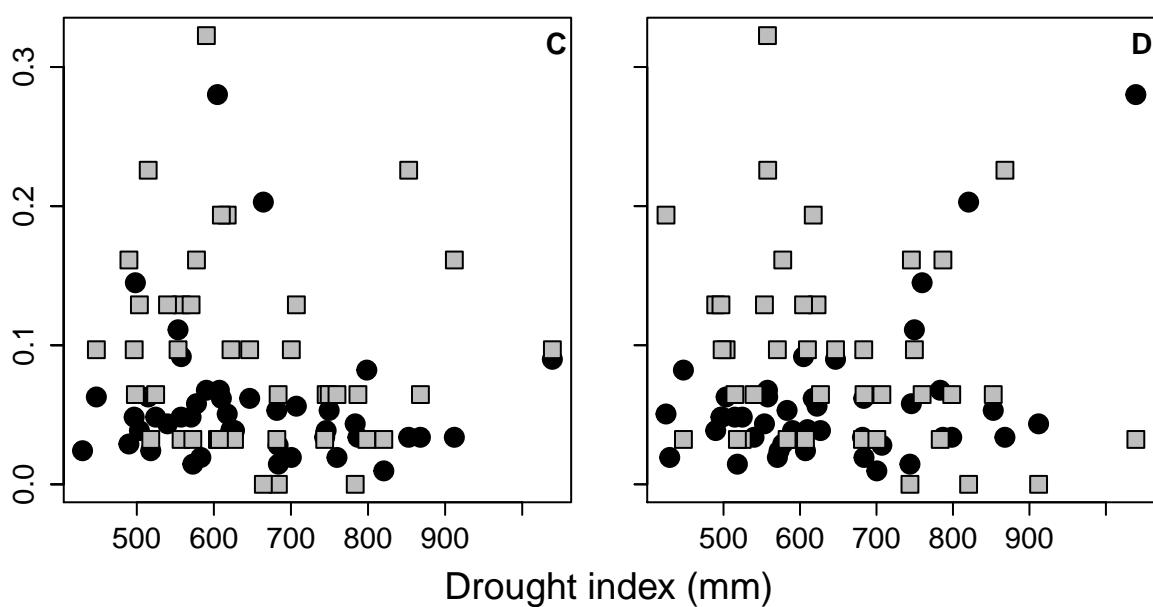
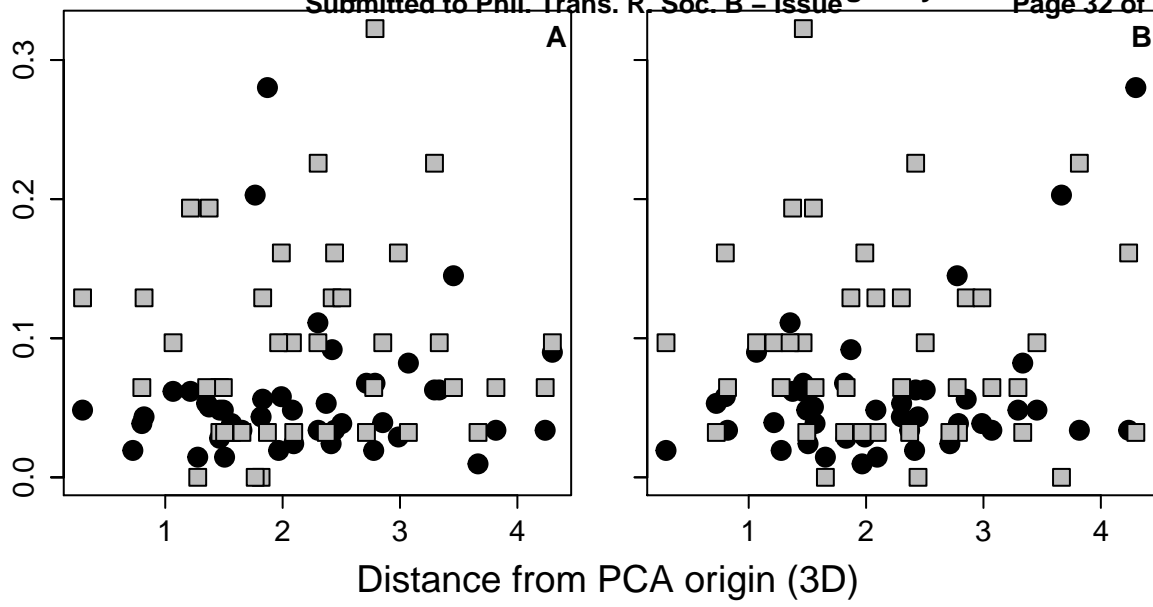
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Proportion of species
Net population explosions (butterflies)
Net population explosions (moths)
Net population explosions (birds)
Net population explosions (Lepidoptera)





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